THE GENUS TIARELLA IN WESTERN NORTH AMERICA

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This paper treats the three western North American taxa of *Tiarella*, a genus of the Saxifragaceae which is distinguished by two unequal valves of the dehiscent fruits and panicles of white flowers. These taxa have previously been treated as distinct species, recognizable by the basal leaf conformation. Study of the complex by analysis of population samples, field observations, and experimental breeding clearly indicates that there is continuous variation among the three. Their recognition as elements of one species complex, *T. trifoliata* L. is proposed. Within this species, two subspecies, ssp. *unifoliata* and ssp. *trifoliata* with two varieties, var. *trifoliata* and var. *laciniata*, are recognized.

DISTRIBUTION. The most widely distributed of the three, ssp. *unifoliata* has its eastern boundary in western Alberta and western Montana. From Alaska it extends southward, along both sides of the Cascade range, to the Santa Cruz Mountains in California. In California, it grows as low as at 150 feet elevation, whereas in most other areas it is found growing in moist forests in the mountains above 2000 feet.

Subspecies *trifoliata* is centered primarily west of the Cascade Mountains in Washington, but extends from Alaska to southern Oregon and to eastern British Columbia, and is found in scattered localities in western Montana, Idaho, and eastern Washington. It occurs in unmixed stands in western Washington at elevations less than 1500 feet.

Subspecies *trifoliata* and *unifoliata* both occur, mostly at altitudes that are mutually exclusive, along the western slopes of the Cascade range from Skamania Co. to Whatcom Co. in Washington and also in southwestern and eastern British Columbia. The ranges of the two, however, often overlap above 1500 feet elevation. Between 1500-2000 feet, ssp. *trifoliata* seems to be the more frequent, whereas ssp. *unifoliata* is the more frequent above 2500 feet. In their area of overlap, intergradient plants are evident.

Variety *laciniata* is narrowly limited to Vancouver Island, and to the San Juan and other adjacent islands of Puget Sound. Plants which closely approximate var. *laciniata* occur sporadically with mixed populations of ssp. *trifoliata* and *unifoliata* on the mainland. Variety *laciniata* appears always to be sympatric with var. *trifoliata*.

CYTOLOGY AND HYBRIDIZATION. All three taxa were found to have a gametic chromosome number of 7.

Controlled pollinations gave evidence that all were self-compatible, although none was spontaneously self-pollinating. All possible crosses resulted in fruits in percentages ranging from 40–65% (in 1963) or 45—88% (in 1964). Reciprocal crosses between var. *trifoliata* and var. *laciniata* yielded especially high percentages of fruit set (Kern, 1964).

No differences in the embryo and endosperm, or in seed-size, could be detected between seeds collected in the field and those produced by artificial pollinations. However, neither the seed produced from artificial pollinations nor that collected in the field germinated, possibly because it was stored for five months before planting. Numerous seedlings were observed in the field, so apparently germination readily occurs in the natural populations.

Morphological Study of the Leaves. Local population samples of 30–100 mature plants were taken from fifteen different locations in the Northwest. The plants were pressed in the usual manner but were left unmounted. The collections were used in the following ways: 1, for a series of simple leaf measurements; 2, for the portrayal of variability within a single population, 10–15 extreme and intermediate forms from each population were photographed; 3, for the construction of polygonal graphs showing intra- and inter-populational variation of leaf pattern; and 4, for the construction of a bar graph designed to detect hybridization between the extreme forms (Anderson, 1941).

1. *Leaf-sinus measurements.* In order to obtain a precise assessment of morphological differences, a series of linear (fig. 1) and vein-angled measurements was made on the three largest basal leaves from each dried plant. The method of measuring the depth of lobation was an indirect one of measuring the length of the line forming a right angle with the midrib and extending straightway to the base of the sinus between the lobes. Approximately fifty plants per population (150 leaves) were measured.

The measurements of depth of lobation (numbers 10, 11, and 12 in fig. 1) were the only ones that might be interpreted to indicate a discontinuity between taxa. Measurement number 12, the depth of the sinus which splits the single leaf into three leaflets with distinct petiolules, readily separates the unifoliate from the trifoliolate plants even though there is a continuous gradation in the depth of the sinus (Kern, 1964). No true discontinuity exists in the increasing depth of the sinuses between the lobes of the unifoliate leaves and the spaces which these sinuses ultimately become in those plants with trifoliolately compound leaves. The critical mean leaf-sinus measurements, nos. 10–12 (fig. 1), are given in Table 1. All measurements are given in centimeters.

2. *Variability within populations.* Although unmixed populations of either ssp. *trifoliata* or *unifoliata* showed some variation from leaf to leaf, any one of the leaves in each could be readily identified as belonging to one or the other of these two taxa.

Populations with mixtures of plants with unifoliate, trifoliolate, and laciniately incised leaves presented a more complex problem. Nine mass collections of 30–100 plants were made along the western slopes of the Cascade Range from Mt. Rainier National Park north to Mt. Baker National Forest. Four of these will be reviewed below (Kern, 1964).

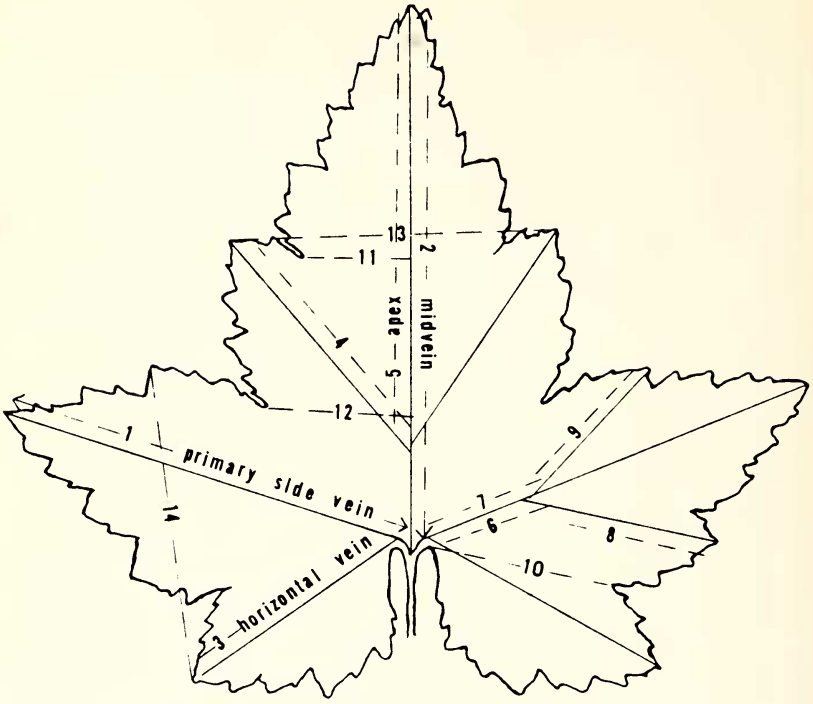

FIG. 1. *Tiarella* leaf showing measurements and enumerations used.

Plants of Denny Creek, about five miles west of Snoqualmie Pass, Washington, were representative of a population where the unifoliate phase was the most frequent. In the mass collection, 24 plants could definitely be called ssp. *unifoliata,* 12 ssp. *trifoliata,* 2 var. *laciniata,* and 13 intermediate between ssp. *trifoliata* and *unifoliata.* The plants that were considered intermediate all had some indentation toward the midvein. The range was from a slight indentation to a lobation as deep as that seen in plants misidentified as *T. trifoliata,* even though the apical and lateral lobes do not have distinct petiolules. Plants with such deeply dissected leaves are comparable to those that Lakela (1937) refers to as *T. unifoliata* f. *trisecta,* since they are very deeply dissected toward the midvein, but without distinct petiolules. All plants without distinct petiolules are considered here as unifoliate rather than trifoliolate phases.

There were a few plants in this population that could be called var. *laciniata,* although they had larger and less-deeply dissected leaves than those characteristic of var. *laciniata* of the San Juan Islands.

Mixed populations of ssp. *unifoliata* and ssp. *trifoliata* which were linked by intergradient forms were found in numerous locations, only three of which are pictured (fig. 2 A–C).

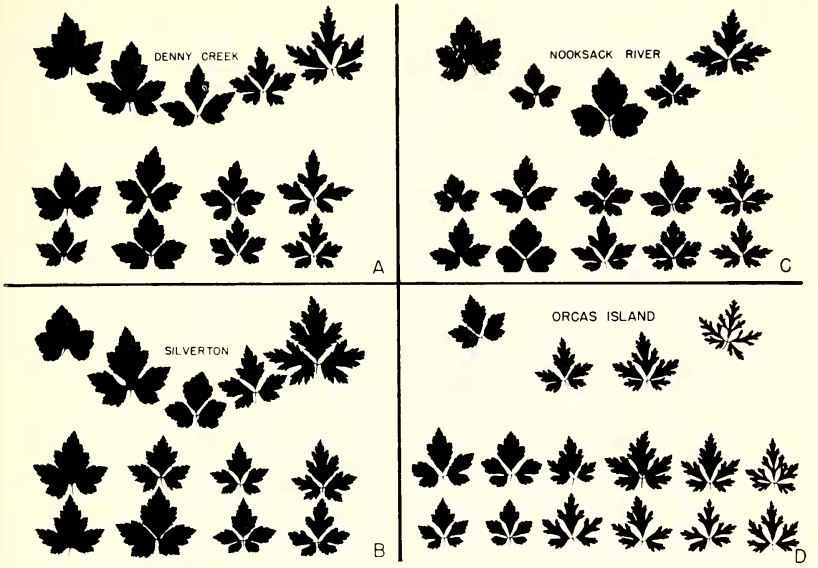

FIG. 2. Leaf outlines showing the range of variation within the population. The leaves in the upper two corners represent the extreme phases with intergradient forms between. The bottom two rows represent a portion of the variability within the population: A, Denny Creek, King Co., Wash.; B, Silverton, Snohomish Co., Wash.; C, Nootsack River, Skagit Co., Wash.; D, Orcas Island, Island Co., Wash.

The variation in leaf character becomes greatly complicated in the San Juan Island populations. On Whidbey I. and Orcas I., var. *laciniata* occurs in almost equal numbers with var. *trifoliata* in the moist woodland. On Orcas I. (fig. 2D), there are so many intergradient forms that the majority do not fit in either category.

3. *Intra- and inter-populational variation of leaf pattern.* The variation within a population may be portrayed by the polygonal graph method (Davidson, 1947). As stated by Davidson, the graph "consists of a circle, with as many radii as there are characters to be compared. The characters, measured along each radius, are assigned absolute, relative, or arbitrary values. The characters possessed by each specimen are plotted along each radius, and the points are joined" (fig. 3A). By the overlap, or non-overlap, of the separate polygons on each graph, one can determine continuous or non-continuous variation. This would indicate whether a population contains two or more segregates or merely one variable entity. Eight characters, either absolute or relative, are graphed in fig. 3B–D.

Figure 3B, as indicated by the normal distribution (Davidson, 1947) on all radii, shows very little variability in an unmixed population of subsp. *unifoliata*. Polygons of a mixed population of var. *trifoliata* and

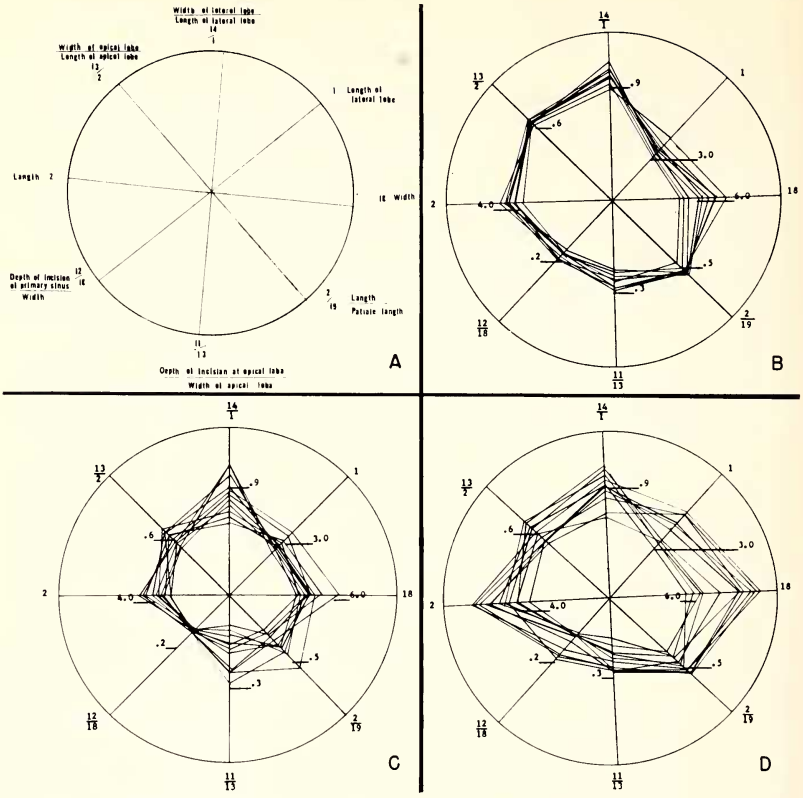

FIG. 3. Polygonal graphs for comparison of patterns of several characters: A, form used for the polygonal graphs, showing the basis for the graphing of eight characters; B, unmixed populations of ssp. *unifoliata;* C, mixed population of var. *trifoliata* and var. *laciniata;* D, mixed populations of ssp. *unifoliata;* ssp. *trifoliata,* var. *trifoliata,* and var. *laciniata.*

var. *laciniata* from Orcas I. (fig. 3C) show normal variability on all radii, indicating that there are numerous intergradient forms from one extreme (the trifoliolate phase) to the other (the laciniate phase).

A single mixed population from Denny Creek is graphed in fig. 3D. The variability on the radii for depth of primary sinus/width (12/18) and *depth of incision of apical lobe*/width of apical lobe (11/13) indicates the total range of variation within the population. From this and other patterns of continuous variation, it is evident that the mixed populations form one variable entity.

4. *Hybrid index.* The hybrid index presents the tabular data in a single figure. To each of three leaf measurements an index number was assigned (table 2). The numbers were then totaled to obtain the index value. The bar graph (fig. 4) was constructed with these values plotted against their frequency within the populations.

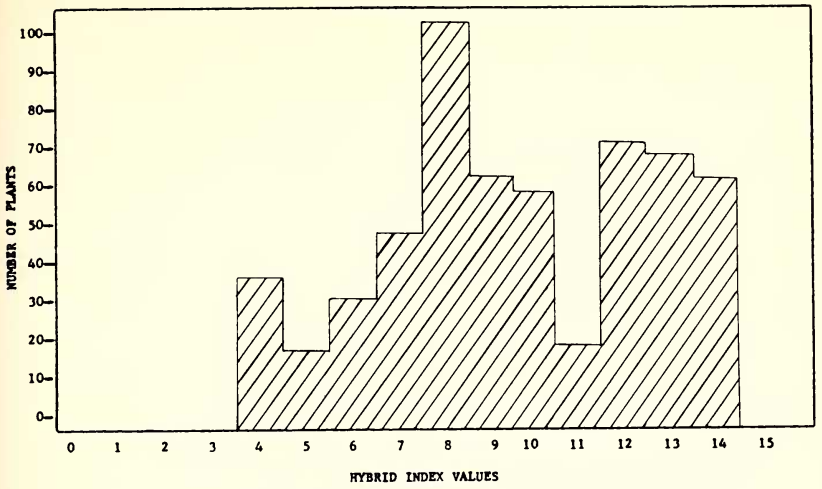

FIG. 4. Bar graph of hybrid index values for the taxa of *Tiarella*.

The index value of 4 is typically that of var. *laciniata,* 8 that of var. *trifoliata,* and 14 that of ssp. *unifoliata*. It can be seen that three peaks, at 4, 8, and 12–14 occur. There is a distinct decrease of frequencies at index value 11; intermediates at this value are not as numerous as those more closely resembling either the trifoliolate extreme (8) or the unifoliate extreme (12–14).

No sharp decrease of frequencies between index values 4 and 7 can be noted; the range of variation from var. *laciniata* to var. *trifoliata* appears to be continuous.

TAXONOMIC CONSIDERATIONS. As shown by controlled breeding experiments and by strong circumstantial field evidence, the taxa of *Tiarella* are freely interbreeding. The flower and fruit structures of the taxa are indistinguishable. The various and variant attributes of leaf morphology remain as the only bases for assessing discontinuities. From the evidence presented above, no sharply discontinuous variation can be found. Therefore, I consider the western populations of *Tiarella* to constitute a single polymorphic species—*T. trifoliata* L.

The partial discontinuity in geographical distribution and morphology is sufficient, however, to justify the recognition of infraspecific elements. The unifoliate and trifoliolate taxa of *Tiarella* are here considered to be of subspecific rank. Each occupies a major geographical area of the species range, and the two have an area of overlap, at elevations ranging between 2000–4500 feet, where they intergrade more or less completely.

The laciniate-leaved phase, var. *laciniata,* occurs sporadically with mixed populations on the mainland but occurs in approximately equal numbers with the trifoliolate phase in insular populations. It, as found on the mainland, is possibly simply the result of recurrent and sporadic

Table 1. Leaf-sinus Measurements for the Taxa of Tiarella

Taxa	No. of plants	Measurement Number 10 mean	10 range	11 mean	11 range	12 mean	12 range
ssp. *unifoliata*	24 (Denny Cr.)	2.1	1.3–2.6	1.1	0.5–1.6	1.5	0.8–2.1
	24 (Silverton)	1.8	1.1–2.2	0.9	0.6–1.2	1.3	0.9–1.8
	10 (Nooksack R.)	1.8	1.0–2.2	1.0	0.5–1.3	1.3	0.8–1.6
Intermediate	13 (D.C.)	2.2	1.9–3.0	1.0	0.7–1.2	0.4	0.1–0.9
	9 (Sil.)	2.1	1.7–2.5	1.1	0.8–1.2	0.4	0.1–0.9
	9 (Nook.)	1.3	1.1–1.7	0.6	0.6–0.7	0.4	0.2–0.6
var. *trifoliata*	12 (D.C.)	1.0	0.6–2.6	0.6	0.4–0.9	0	
	15 (Sil.)	1.0	0.6–1.5	0.7	0.4–0.9	0	
	36 (Nook.)	1.2	0.4–2.4	0.7	0.5–1.2	0	
	25 (Orcas Island)	1.3	0.7–1.7	0.5	0.4–0.8	0	
var. *laciniata*	2 (D.C.)	0.1		0.3		0	
	2 (Sil.)	0.8	0.4–1.3	0.4	0.3–0.6	0	
	2 (Nook.)	0.6	0.3–0.8	0.4	0.3–0.5	0	
	25 (O.I.)	0.1	0.1–0.5	0.1	0.1–0.2	0	

recombination of recessive genes. These individuals are of limited occurrence in a population and apparently cannot establish themselves as a major segment of the species.

Therefore, in *T. trifoliata* L., two subspecies are recognized: ssp. *trifoliata,* with two varieties, *trifoliata* and *laciniata* (Hooker) Wheelock, and ssp. *unifoliata* (Hooker) Kern. The appropriate new combination is hereby proposed.

Systematics. Tiarella trifoliata L. Sp. Pl. 406. 1753.

Blondia trifoliata Raf. Fl. Tell. 2:75. 1836. *T. rhombifolia* Nutt. in Torr. & Gray, Fl. N. Am. 1:588. 1840. (*G. Demidoff,* "Habitat in Asia boreali".) According to Hultén (Fl. of Alas. and Yukon 5:943. 1945) the actual type was: *Steller,* Cape St. Elias, Kayak I., Alas.

T. stenopetala Presl, Rel. Haenk. 2:55. 1831. (*Haenke,* "Nootka-Sund".)

T. trifoliata var. *laciniata* (Hook.) Wheelock, Bull. Torrey Club 23:72. 1896. *T. laciniata* Hook. Fl. Bor. Am. 1:239. 1832. *Petalosteira laciniata* Raf. Fl. Tell. 2:74. 1836. (*Menzies,* "North-West coast of America".)

Table 2. Hybrid Index Values

Character	Range	Index Number
Depth of incision of apical lobe (measurement #10)	0.1–0.2	1
	0.3–0.9	2
	1.0–1.6	3
	1.7–3.0	4
Depth of incision of lateral lobe (measurement #11)	0.1–0.2	1
	0.3–0.4	2
	0.5–0.9	3
	1.0–1.7	4
Depth of incision between primary and lateral lobes (measurement #12)	0	2
	0.1–0.9	4
	1.0–2.0	6

T. trifoliata ssp. **unifoliata** (Hook.) Kern, com. nov. *T. unifoliata* Hook. Fl. Bor. Am. 1:238. 1832. *Petalosteira unifoliata* Raf. Fl. Tell. 2:74. 1836. *Heuchera californica* Kell. Proc. Calif. Acad. 5:53. 1873. *T. unifoliata* var. *procera* A. Gray, Bot. Calif. 1:199. 1876. *T. trifoliata* var. *unifoliata* Kurtz, Bot. Jahrb. 19:378. 1894. *T. californica* Rydb. N. Am. Fl. 22:118. 1905. (*Drummond,* "Height of land in the Rocky Mountains, near the source of the Columbia, and at Portage River")

T. unifoliata f. *trisecta* Lakela, Am. Jour. Bot. 24:350. 1937. (*Butters & Holway 216c,* Beaver Valley, Alta.) = ssp. *unifoliata.*

Perennial, rhizomatous herbs; flowering stems 10–60 cm high; cauline leaves 2–3, short-petioled; basal leaves simple to compound; inflorescence paniculate; flowers white, sometimes with a pinkish tinge; sepals 5, oblong to triangular, 2–5 mm long, somewhat irregular, the hypathium short-campanulate, ¼–½ as long as the lobes, almost free of the ovary; petals 2–5 mm long, subulate, almost indistinguishable from the filaments; stamens 10, 2–6 mm long, those opposite the petals the shorter; pistil 1-celled, with two parietal and nearly basal placentae; valves of the capsule unequal, the upper one ⅓ as long as the lower; seeds 1.5–2.0 mm, black, shining and smooth, the raphe prominent. The species consists of two subspecies and two varieties as follows:

Leaves simple, 4–12 cm broad, 2.5–7.0 cm long (including those plants with leaves dissected to within 0.1 cm of the midvein but without distinct petiolules) ssp. *unifoliata* (Hook.) Kern

Leaves compound, 2–12 cm broad, 2.5–7.0 cm long.....ssp. *trifoliata*

Leaflets laciniately cleft, the lateral pair deeply dissected to within 0.1–0.4 cm of the midvein, the middle one dissected to within 0.1–0.9 cm of the midvein; occurring as a sporadic variant with ssp. *unifoliata* and ssp. *trifoliata* and sympatrically with ssp. *trifoliata* on Vancouver Island and adjacent islands of Puget Sound.....var. *laciniata* (Hook.) Wheelock

Leaflets not laciniately cleft, the lateral pair shallowly lobed to lobed within 0.5 cm of the midvein, lobes of the middle leaflet dissected to within 1.0 cm of the midvein; occurring primarily west of the Cascade Range in Washington, but ranging from Alaska to Oregon and east to eastern B.C.....var. *trifoliata*

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NOTES AND NEWS

Occurrence of the Genus Euphrasia in the Pacific Northwest.—The genus *Euphrasia* has not previously been reported from Washington. Now, *E. canadensis* Townsend has been collected in Parkland, near Tacoma, Pierce Co., Washington, where it is locally abundant in a moist grassy area adjacent to a small swamp one-half mile east of the intersection of state highways 5 and 512 *(Ganders 135,* WS). *Euphrasia canadensis* is almost certainly introduced at Parkland, and the fact that another localized species, *Viola lanceolata* L., occurs with it suggests the possibility of the same mode of introduction. *V. lanceolata* was introduced in the early twentieth century with importations of cranberry plants from New England and Wisconsin (Schultz, J. H., Madroño. 8:191–193. 1946), and since *E. canadensis* occurs in New England this same thing could have occurred. However, if this is the case, it is surprising that the plant has not been collected before in Washington, as *V. lanceolata* was detected in 1936 (Jones, G. N., Madroño. 4:34–37. 1937). Another record for *Euphrasia* that should noted is a collection of *E. americana* Wettst. from Qualicum, Vancouver I., British Columbia (on golf links, *Redfern,* WS). This species was not included in *Vascular Plants of the Pacific Northwest.*—Fred R. Ganders, Washington State University, Pullman.

Herbarium Supplies.—Bonestell & Co., of San Francisco, for many years a supplier of herbarium supplies, has recently been forced to go out of business. The line of herbarium supplies developed by Mr. Cyril A. Cross, in consultation initially with Dr. LeRoy Abrams and Dr. W. L. Jepson, is now available through the Commercial Paper Corp., 300 Brannon St., San Francisco, California 94107. Mr. Cross will handle these supplies at the Commercial Paper Corp. and he has indicated that the same high standards will prevail and that the prices will be the same as they were as of September 15, 1965.